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A comparison of three methods of trapping saproxylic beetles

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Abstract. A high trapping efficiency was found both for window traps and trunk-window traps, while the efficiency of extraction cylinders was low. Trunk-window traps are suitable for comparison of different substrates within the same forest environment, while comparative studies of different forest environments are more difficult, due to baiting effects. Window trap captures are more suitable for comparing different forest environments, but are related to ecological conditions over wide areas, and are almost unaffected by substrate conditions in the near surroundings of the traps.

INTRODUCTION

An increased interest in species conservation in recent years has increased the need for studies of forest-dwelling beetles, especially obligate saproxylic beetles depending on decaying wood or wood-inhabiting fungi for development. Comprehensive studies of saproxylic beetles have been made for the purpose of ecological research (Väisänen et al., 1993; Ås, 1993; Kaila et al., 1994; Siitonen, 1994; Siitonen & Martikainen, 1994; Økland et al., 1996), and additional studies may be initiated in connection with future plans for monitoring biodiversity, and the demand for more ecological information to promote a sustainable forest management (Noss, 1990; Reid et al., 1993).

Many methods have been applied for sampling forest-dwelling beetles (see for example: Browne, 1978; Hosking, 1979; Chandler, 1987; Biström & Halme, 1988; Biström & Väisänen, 1988; Chandler, 1991; Muirhead-Thomson, 1991; Chandler & Peck, 1992; Owen, 1992; Schmitt, 1992; Kaila, 1993; Kaila et al., 1994; Siitonen, 1994). For collecting saproxylic beetles, techniques of rearing or extracting from wooden substrates have a long tradition (Saalas, 1917; Palm, 1951, 1959; Väisänen et al., 1993). In comparison with flight traps, these methods have the advantage of sampling directly from the microhabitats. However, the different methods applied have proved to be unsatisfactory in many respects. Rearing or collecting beetles directly from dead wood substrates are difficult to standardize, and even with a large sampling effort most species are too infrequent for statistical comparisons (Kaila, 1993; Siitonen, 1994). With bark peeling and sifting much habitat is destroyed, and species inside the wood are under-represented (Ås, 1993; Väisänen et al., 1993; Siitonen, 1994).

Flight-interception traps do not give exact information about the microhabitat of larval development, but they are many times more efficient in comparison with extraction methods. Window traps are considered particularly suitable for trapping saproxylic beetles, and have been used in several studies (Bakke, 1975; Stokland, 1994; Siitonen, 1994; Økland et al., 1996). Large numbers of saproxylic beetles are also trapped by the newly developed trunk-window trap (Kaila, 1993), or variants of this trap model (Bakke & Kvamme, 1993; Økland & Hågvar, 1994).

Basic knowledge of the efficiency and selective properties of the single methods for sampling saproxylic beetles is insufficient. Such knowledge is considered fundamental for the choice of methods and the interpretation of results in future studies. The present study compared three methods of trapping saproxylic beetles within the same locality of spruce forest: (1) window traps (free-hanging), (2) trunk-window traps (on polyporous fungi) and (3) extraction cylinders (emergence traps mounted on dead trunks). Trapping efficiency, selectivity, sample variation and spatial range of environmental influence were evaluated for each trap model. The application of these trap models is discussed on the background of present findings, and former experience with corresponding methods.

METHODS

Study area

The study was performed within an area of about 160 km of continuous forest in Østmarka (UTM: 32VPM1436, 59°51′N 10°57′E, about 15 km southeast of Oslo) in Norway. The landscape is intersected by many small north-south valleys with only slight variation in elevation (200 to 300 metres above sea level). Gneisses make up the bedrock. Most of the area is covered by spruce forest (*Picea abies*) with scattered deciduous trees (*Betula* sp., *Populus tremula*, *Salix caprea*, *Sorbus aucuparia*, *Alnus incana*, *Prunus padus*), except for a dominance of pines (*Pinus sylvestris*) on ridges and hill tops. The density of decaying wood shows considerable variations within the study area. More details about the study are given in Økland et al. (1996).

Comparison of trapping methods

All traps were operated within two similar sites of spruce-dominated forest in a forest reserve in the centre of Østmarka forest (referred to as site 1 and site 2). Both sites contained large numbers of windfalls. The distance between the sites was about 900 m. All three trap types were restricted to the same area of about 0.3 ha in each site:

THE WINDOW TRAP (Siitonen, 1994; Økland et al., 1996) is a flight interception trap, based on the principle that flying individuals hit a transparent "window" and fall into a collecting funnel. In the present study, the trap consisted of two transparent cobex plates (21 x 39 cm) mounted above a 22 cm wide plastic funnel (Fig. 1A). A cup with preservative fluid was mounted below the funnel, and two small holes halfway up the cup wall allowed surplus water to escape during rainfall. A roof was attached to prevent litter and rain water from falling into the trap. Each trap hung from a slanted bamboo pole with the trapping surface 0.7–1.0 m above the ground. In each site, 25 traps were placed in a square grid, with a distance of 2.5 m between neighbouring traps.

THE TRUNK-WINDOW TRAP (Kaila, 1993; Bakke & Kvamme, 1993; Økland & Hågvar, 1994) shares the same principle as the window trap, but this trap is attached to dead tree trunks, preferably close to sporocarps of polyporous fungi, or by placing the "window" in a vertical slit cut through the sporocarp. The sporocarp is not damaged as the slit heals after removal of the plate. The present variant of this trap consisted of the same components as the window trap described above, except that it had only one vertical transparent cobex plate (20 x 20 cm) (Fig. 1B). The funnel was adjusted to fit closely to the trunk below the sporocarp. In each of the two sites, 15 traps were mounted on living sporocarps of *Fomitopsis pinicola* (Fr.) Karst. on dead spruce (*Picea abies* [L.] Karst). With only a few exceptions, all traps were mounted on standing trunks. Mean distance between the traps was about 10 m.

THE EXTRACTION CYLINDER is based on the principle of rearing out insects developing or hibernating in a piece of decaying wood. The design of the extraction cylinders was developed for the present study; however, the principle is much the same as in the "Totholz-eklektor" applied in some German studies (Albrecht, 1990; Schmitt, 1992). Each trap enclosed a 75 cm section of a dead spruce trunk (*P. abies*), and a black cotton cloth was used (Fig. 1C). Space between the trunk and the textile was formed by arches of 3 mm wire inserted into the trunk surface. The ends of the cotton cylinder were closed by thin wire. Two glass collecting vials were attached to the lower part of each cylinder. Ethylene-glycol with a small

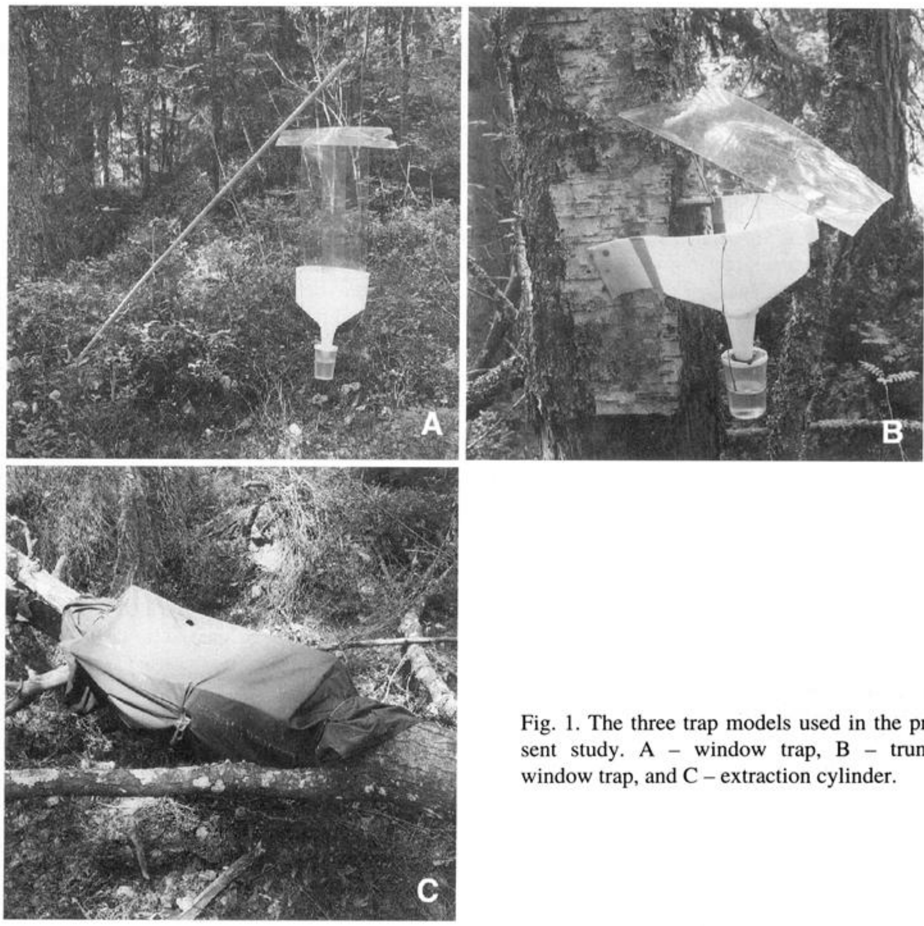


Fig. 1. The three trap models used in the present study. A – window trap, B – trunk-window trap, and C – extraction cylinder.

amount of detergent was used as preservative in all trap models. Altogether, 167 extracting cylinders were mounted on spruce logs, 98 traps in site 1 and 69 traps in site 2. Logs were selected randomly among spruce logs of varying condition, ranging from superficial to thorough decay, and with a minimum diameter of 20 cm. All trap types were operated from 28 April to 6 September 1992. During this period, window traps and trunk-window traps were emptied four times, while extracting cylinders were emptied twice.

Spatial range of environmental influence

In 32 sites of Østmarka forest, window trap captures of obligate saproxylic beetles were compared with the density of decaying wood at various recording scales in the surrounding forest. All sites were positioned in old spruce forest (> 80 years) of *Eu-Piceetum myrtilletosum* vegetation type (Fremstad & Elven, 1987) representing different densities of decaying wood. Within each site, beetles were trapped by ten window traps placed in a pre-determined circle (diameter 20 m). The traps were operated from 22 April to 13 September 1991 and emptied four times. The density of decaying wood surrounding each trapping site was estimated for squares of different dimensions (0.1–128 ha) by means of 5 m-broad transects through the site centres.

Taxonomical and statistical treatment

All beetles were identified to species level, using the nomenclature of Silfverberg (1992). In some of the comparisons, beetle species were divided into functional groups, defined as follows:

(i) obligate saproxylic species – those dependent exlusively on dead wood or wood-inhabiting fungi for development;

(ii) facultative saproxylic species – those associated with dead wood or wood-inhabiting fungi, but that may breed in other habitats;

(iii) species in newly dead wood – those associated with weakened or recently dead trees (0–1 year);

(iv) species in early decayed wood – those associated with dead trees in initial decomposition, with decay less than 5 cm deep;

(v) species in strongly decayed wood – those associated with deeply decayed wood (> 5 cm deep) or wood decayed thoroughly;

and (vi) species associated with polypores – those species reared from polypores, or frequently observed feeding on polypores (mycophages or predators).

Biological information for the classification of beetle species was derived from a database compiled by J. Stokland (pers. comm.), from the literature (Koch, 1989–92), and from studies within the same area (S. Hågvar, pers. comm.).

Red-listed beetles were defined as species present on the Norwegian or Swedish red lists (Størkersen, 1992; Ehnström et al., 1993).

For each trap model, the expected number of species per sample size (number of traps) was estimated by calculating the mean of 100 randomised orders of trap-selection (Figs 2, 3). The same procedure was applied to both traps within the same site, and to the pooled trap material from both sites. Confidence intervals (Figs 2, 3) and standard deviation values (Table 6) were based on the variation between the 100 randomised orders of trap-selection.

All comparisons of species richness and abundances of single species between the trap models were tested by Pearson's chi square statistic for goodness of fit (Bhattacharyya & Johnson, 1977). The tests were limited to examples with a mean of at least five per cell unit. The level of significance was set at 1% in tests of single species in order to reduce the probability of significance by chance in the simultanous tests (Table 3). The significance level was kept at 5% in the other comparisons, since the numbers of simultanous tests were much lower (Tables 1, 2).

The proportion of common species in site 1 and 2 was calculated by Jaccard index, using the formula $Y = a/b$, where a = the number of species shared by the sites, and b = the total number of species.

Relationships between the number of individuals and densities of decaying wood were analysed by Spearman's rank correlation (Freund, 1992), and were considered significant at a 5% level. The influence of density of decaying wood on species richness was analysed by simple linear regression (Weisberg, 1985).

RESULTS

General trap efficiency

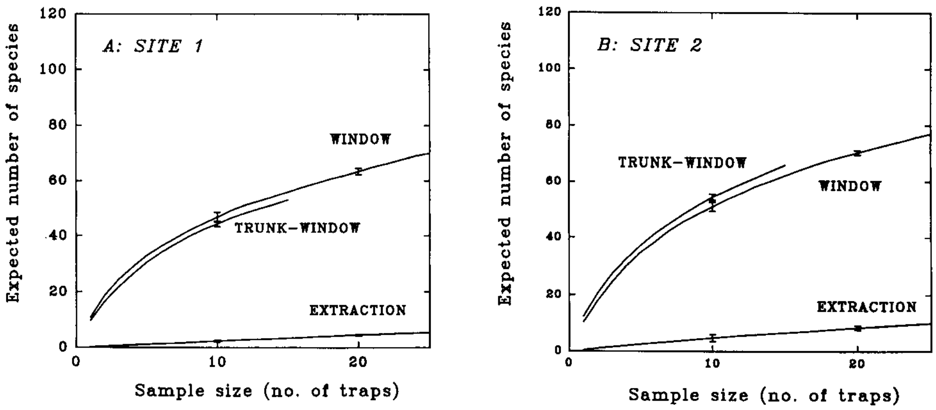
In the comparison of trap models, the window traps (n = 50) collected 266 beetle species (1456 specimens), the trunk-window traps (n = 30) yielded 166 beetle species (1449 specimens), and the extraction cylinders (n = 167) trapped 64 species (162 specimens). Species occurring in less than 5% of the traps constituted 60.2% of the species trapped by window traps, 41.6% of the species in trunk-window traps, and 98.4% of the species in extraction cylinders.

The trapping efficiency of the extraction cylinders was low in most respects. In comparison with the other trap models, extraction cylinders yielded a much lower number of both beetles in general and obligate saproxylic beetles (Table 1, Fig. 2). Even when the capture in all 167 extraction cylinders was compared with 30 window traps and 30 trunk-window traps, the number of species and abundance within single species were usually lower, both within different functional groups (Tables 1, 4), and within different families of beetles (Table 2).

TABLE 1. Number of species in different functional groups of beetles trapped by window traps (30 ex.), trunk-window traps (30 ex.), and extraction cylinders (167 ex.), compared by chi-square tests. Significance levels: ns $p > 0.05$, *$p < 0.05$, **$p < 0.01$ and *** $p < 0.001$.

Beetle groups	Window	Trunk-window	Extraction	W-T	W-E	T-E
Obligate saproxylic beetles	88	81	28	ns	***	***
Facultative saproxylic beetles	30	26	12	ns	**	*
Species in newly dead wood	32	25	6	ns	***	***
Species in early decayed wood	35	29	13	ns	**	*
Species in strongly decayed wood	27	26	13	ns	*	*
Species associated with polypores	45	46	17	ns	***	***
Saproxylic flower visitors	25	19	7	ns	**	*
Saproxylic predators	31	25	10	ns	**	*
Red-listed beetles	3	6	2	ns	ns	ns
All beetle species	209	166	64	*	***	***

Both window traps and trunk-window traps showed a high efficiency in trapping beetle species. With thirty traps, these models yielded 9–11 times more beetle species than a corresponding number of extraction cylinders. The total number of beetle species was significantly higher for window traps compared to trunk-window traps (Table 1), but the number



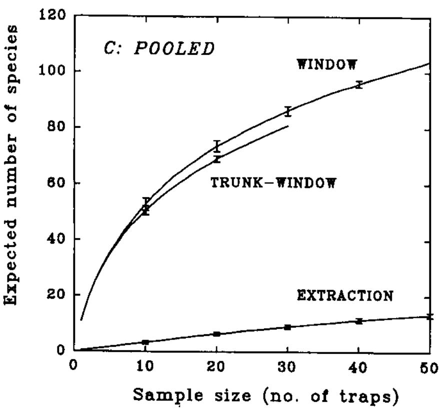


Fig. 2. Expected number of obligate saproxylic species in relation to sample size (number of traps) for window traps, trunk-window traps, and extraction cylinders within (A) site 1, (B) site 2, and within both sites pooled (C). Vertical lines = 95% confidence intervals.

TABLE 2. The number of species in different families of beetles trapped by window traps (30 ex.), trunk-window traps (30 ex.), and extraction cylinders (167 ex.), compared by chi-square tests. Significance levels are given in Table 1.

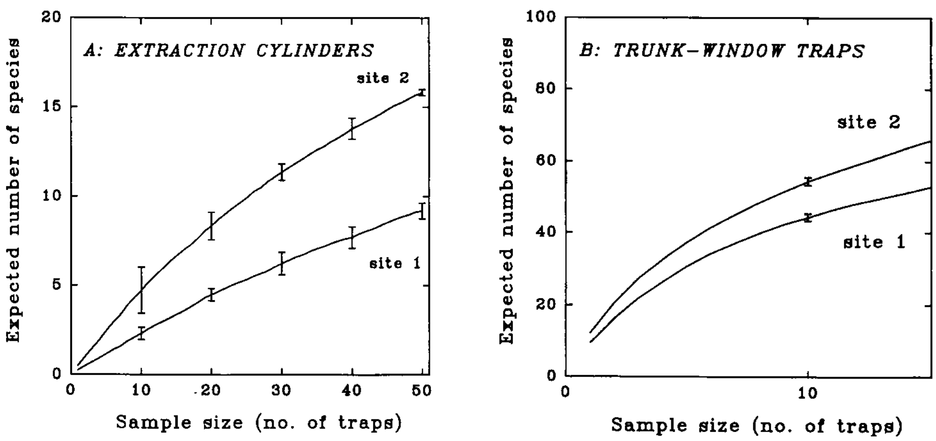
Family	Window	Trunk-window	Extraction	W-T	W-E	T-E
Carabidae	6	6	6	ns	ns	ns
Haliplidae	1	0	0			
Dytiscidae	3	0	0			
Hydrophilidae	0	1	1			
Ptiliidae	0	1	0			
Leiodidae	3	9	2	ns		*
Silphidae	1	1	1			
Cholevidae	2	2	2			
Scydmaenidae	1	2	2			
Staphylinidae	73	50	16	*	***	***
Pselaphidae	4	1	3		ns	
Sphaeritidae	1	0	0			
Histeridae	0	2	0			
Scirtidae	1	0	0			
Scarabaeidae	3	1	0			
Lycidae	1	2	1			
Cantharidae	3	9	2	ns		*
Elateridae	9	7	4	ns	ns	ns
Eucnemidae	0	1	1			
Buprestidae	1	1	0			
Byrrhidae	1	0	0			
Anobiidae	1	2	1			
Ptinidae	1	1	0			
Lymexylidae	1	1	0			
Trogositidae	1	2	1			
Cleridae	1	0	0			
Melyridae	1	0	0			
Nitidulidae	9	11	1	ns	*	**
Sphindidae	1	0	0			
Rhizophagidae	1	2	0			
Cucujidae	2	0	1			
Cryptophagidae	16	11	5	ns	*	ns
Cerylonidae	3	1	0			
Endomychidae	0	1	0			
Coccinellidae	1	0	0			
Corylophidae	0	1	0			
Latridiidae	9	4	3	ns	ns	ns
Byturidae	1	1	0			
Ciidae	7	7	3	ns	ns	ns
Colydiidae	1	0	0			
Oedemeridae	1	0	0			
Salpingidae	2	1	0			
Tenebrionidae	1	0	0			
Anaspididae	3	2	2			
Mordellidae	1	2	0			
Melandryidae	2	3	0			
Cerambycidae	7	3	0	ns	**	
Chrysomelidae	1	0	0			
Attelabidae	0	1	0			
Curculionidae	6	5	3	ns	ns	ns
Scolytidae	12	8	3	ns	*	ns

of obligate saproxylic species did not differ significantly between these trap types (Fig. 2, Table 1). At 30 traps, the slope of the species-per-trap curve of obligate saproxylic species was 1.11 species per trap for the window traps, and 1.01 species per trap for the trunk-window traps (Fig. 2C).

Selectivity

Considering different functional groups, there was only a small variation in species numbers between window traps and trunk-window traps (Table 1). None of these differences proved to be significant by chi-square testing. Grouping the species into families, only species richness of Staphylinidae showed a significant difference between window traps and trunk-window traps (Table 2).

More pronounced differences were recorded at the species level. Altogether 27 beetle species varied significantly between window traps and trunk-window traps (Table 3), some with marked differences. Many of the species that were more abundant in trunk-window traps are species associated with polypores (Tables 3 and 4). This category includes either species which have been reared from polypores (*Cis glabratus* Mellie and *Cis quadridens* Mellie; Økland & Hågvar, 1994), or frequent visitors under the hymenium



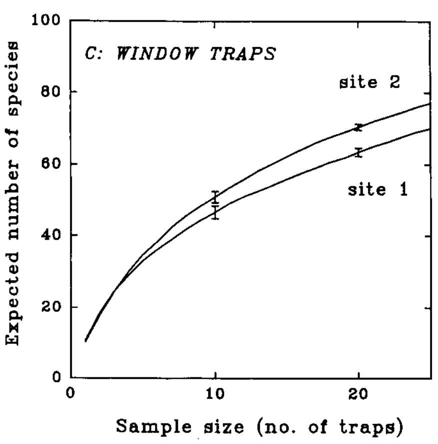


Fig. 3. Expected number of obligate saproxylic species in relation to sample size compared between site 1 and 2, by means of (A) extraction cylinders, (B) trunk-window traps, and (C) window traps. Vertical lines = 95% confidence intervals.

TABLE 3. Beetle species showing significant differences between window traps (W, 30 ex.) and trunk-window traps (T, 30 ex.): p = significance level by chi-square tests; ns $p > 0.01$, **$p < 0.01$ and ***$p < 0.001$.

Family	Species	W	T	p
Carabidae	*Pterostichus oblongopunctatus*	0	2	
Leiodidae	*Anisotoma humeralis*	6	12	ns
Staphylinidae	*Anthophagus omalinus*	11	4	ns
	Atrecus pilicornis	10	0	**
	Gyrophaena boleti	2	330	***
	Leptusa pulchella	15	9	ns
	Lordithon lunulatus	2	179	***
	Lordithon thoracicus	1	12	**
	Oxypoda alternans	5	96	***
	Quedius plagiatus	9	10	ns
Pselaphidae	*Bibloporus bicolor*	36	5	***
	Euplectus punctatus	17	0	***
Elateridae	*Athous subfuscus*	19	7	
	Melanotus castanipes	12	7	ns
Ptinidae	*Ptinus subpilosus*	11	24	
Melyridae	*Dasytes niger*	15	0	***
Nitidulidae	*Epuraea variegata*	2	44	***
Rhizophagidae	*Rhizophagus dispar*	0	45	***
Cryptophagidae	*Antherophagus nigricornis*	0	10	**
	Atomaria alpina	4	25	***
	Atomaria ornata	11	0	***
	Cryptophagus abietis	35	1	***
	Cryptophagus scanicus	3	17	**
	Henoticus serratus	13	0	***
	Pteryngium crenatum	0	72	***
Cerylonidae	*Cerylon histeroides*	1	10	**
Latridiidae	*Aridius nodifer*	9	5	ns
	Corticaria longicollis	0	43	***
	Enicmus rugosus	36	16	**
	Enicmus testaceus	82	51	**
Ciidae	*Cis glabratus*	1	21	***
	Cis quadridens	3	10	ns
Anaspididae	*Anaspis rufilabris*	10	27	**
Melandryidae	*Xylita laevigata*	6	12	ns
Curculionidae	*Rhyncolus chloropus*	0	10	**
Scolytidae	*Crypturgus hispidulus*	1	10	**
	Crypturgus pusillus	22	0	***
	Dryocoetes autographus	17	4	**
	Hylastes cunicularius	12	6	ns

TABLE 4. Number of species in different functional groups being significantly more abundant in one trap type compared with another (chi-square, $p < 0.01$). W = window traps (30 ex.), T = trunk-window traps (30 ex.), E = extraction cylinders (167 ex.)

Beetle groups	W > T	W < T	W > E	W < E	T > E	T < E
Obligate saproxylic beetles	9	9	12	0	14	0
Facultative saproxylic beetles	2	5	1	0	6	0
Species in newly dead wood	4	3	4	0	4	0
Species in early decayed wood	4	3	5	0	8	0
Species in strongly decayed wood	1	3	2	0	3	0
Species associated with polypores	3	8	4	0	12	0
Saproxylic flower visitors	1	2	2	0	2	0
Saproxylic predators	3	6	4	0	6	0

of the polypores, such as spore eaters (*Gyrophaena boleti* (L.), *Pteryngium crenatum* (F.), *Corticaria longicollis* (Zetterstedt), *Anisotoma humeralis* (F.)) and predators (*Rhizophagus dispar* (Paykull), *Lordithon lunulatus* (L.), *Oxypoda alternans* (Gravenhorst) and *Quedius plagiatus* (Mannerheim)). In other ecological categories of beetles, there was a more even number of species that were either more abundant in trunk-window traps, or more abundant in the window traps (Table 4). Similarly, most family groups contained species with more specimens in trunk-window traps, as well as those more abundant in the window traps (Table 3).

Several species were absent in window traps, but were trapped exclusively by extraction cylinders, or both by extraction cylinders and trunk-window traps (Table 5). However, some of these species were captured in an extensive trapping by window traps and malaise traps within the same area one year earlier (Table 5).

Sample variation

Exact values for the variation between samples cannot be found since the total number of species in the sampling areas is unknown. However, the variation in species richness, calculated by selecting different combinations of traps, may give some idea of the

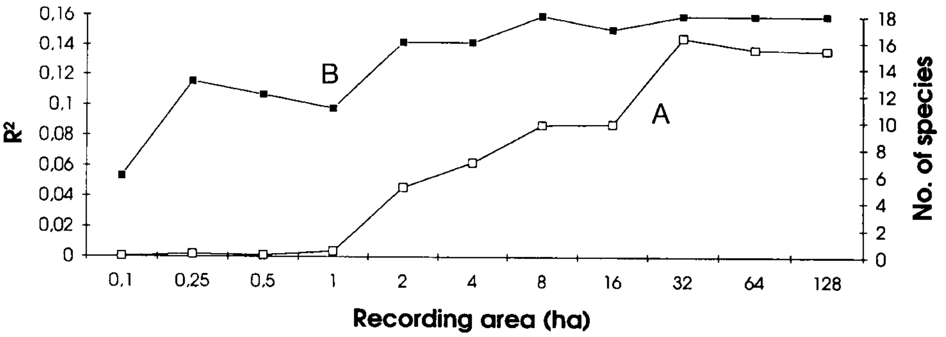


Fig. 4. A – proportion of variability of species richness (R^2) explained by regression on density of decaying wood at different area levels of recording decaying wood, and B – number of species with significant correlation (Spearman Rs) between no. of individuals and density of decaying wood at different area levels of recording decaying wood.

TABLE 5. Species absent in window traps (W), but trapped in extraction cylinders (E), or both extractions cylinders and trunk-window traps (T); no. of specimens. The results were compared to trap material from the preceding season: W91 = captures in 690 window traps operated in the surrounding area of 190 km^2 during 1991 (Økland et al., 1996). M91 = 20 malaise traps opearated in the surrounding area of 190 km^2 during 1991.

Family	Species	1992 traps			1991 traps		Ecological comments
		W	T	E	W91	M91	
Anobiidae	*Anobium punctatum*	0	0	2			wood-boring
Cantharidae	*Malthodes guttifer*	0	0	3		196	under bark, in decayed wood, predator
Carabidae	*Agonum fuliginosum*	0	2	1			reduced wings
	Amara brunnea	0	1	4			forest litter
	Calathus micropterus	0	0	14			reduced wings
	Carabus violaceus	0	4	1			reduced wings
	Pterostichus oblongopunctatus	0	2	10			moist forest litter
	Trechus secalis	0	0	1			detritus, *Sphagnum*, bark
Ciidae	*Cis dentatus*	0	0	2	14		lignicolous fungi, bark, litter
Curculionidae	*Polydrusus undatus*	0	0	1	8	1	various tree species
	Rhyncolus chloropus	0	10	9	13		in decayed wood
Elateridae	*Selatosomus impressus*	0	2	1	62		on trees, bushes
Hydrophilidae	*Megasternum obscurum*	0	0	1			various habitats
Latridiidae	*Corticaria abietorum*	0	0	1			sap, under bark
	Corticaria longicollis	0	43	1			myrmecophile, under bark, rotten wood
Lycidae	*Platycis minuta*	0	0	1		1	decayed wood, stumps
Silphidae	*Pteroloma forsstroemi*	0	0	2	0		moist habitats
Staphylinidae	*Atrecus longiceps*	0	2	4	1		under bark, in decayed wood
	Bolitobius cingulatus	0	0	1	5		in fungi, under bark, predator
	Bolitochara mulsanti	0	0	2	1		lignicolous fungi
	Lathrobium brunnipes	0	2	1			often near vole burrows
	Liogluta letzneri	0	0	1	3		
	Olophrum fuscum	0	2	1	1		moist forest litter
	Othius myrmecophilus	0	1	1			near ant nests, in vole burrows
	Pachygluta ruficollis	0	0	6	99		under bark, ant nests

variability in the captures for each trap model. This measure of variation is affected by the number of traps selected, the number of traps from which they are selected, properties of each site, and properties of each trap model. Table 6 presents the standard deviation in species richness of obligate saproxylic beetles for each trap model when the other sources of variation were kept constant. All trap types revealed a considerable sample variation. Window traps yielded the largest standard deviations, followed by somewhat lower values for trunk-window traps. Standard deviation was lowest for the extraction cylinders. However, sample variation was highest for extraction cylinders when compared with the mean number of species (Table 6).

TABLE 6. A: Standard deviation of species richness for each trap model, achieved by 100 randomized combinations of traps. B: The proportion of common species between site 1 and 2 (Jaccard index) for window traps, trunk-window traps and extraction cylinders. Only obligate saproxylic beetle species were included.

	Window	Trunk-window	Extraction
A: Standard deviation:			
site 1 (5 traps selected randomly from 15 traps)	4.10	3.44	0.95
site 2 (5 traps selected randomly from 15 traps)	4.63	3.54	1.25
pooled (10 traps selected randomly from 30 traps)	5.58	4.42	1.67
Standard deviation in percent of mean species number:			
site 1 (5 traps selected randomly from 15 traps)	12.40	11.22	81.24
site 2 (5 traps selected randomly from 15 traps)	13.30	9.51	50.13
pooled (10 traps selected randomly from 30 traps)	10.56	8.73	50.04
B: Proportion of common species between site 1 and 2	0.41	0.41	0.16

Spatial range of environmental influence

The expected number of species per sample size differed most clearly between two sites for extraction cylinders (Fig. 3A), while the difference was relatively smaller for trunk-window traps (Fig. 3B), and almost negligible for window traps (Fig. 3C). Correspondingly, the similarity in faunal composition between sites was smallest for extraction cylinders, and relatively higher for window traps and trunk-window traps (Table 6B).

In 32 sites with records of the amount of decaying wood, window traps captured altogether 179 species (14,539 specimens) of obligate saproxylic beetles. One-hundred-five species occurring in more than 10% of the sites were tested individually. The density of decaying wood in the near surroundings showed almost no influence on species richness and species abundances of obligate saproxylic beetles (Fig. 4). The influence was increased gradually by increasing the spatial scale of recording decaying wood up to about 30 ha, and remained nearly the same in the interval 32–128 ha. Even with an optimal influence, local trap captures of saproxylic beetles showed relatively weak relationships with density of decaying wood.

DISCUSSION

Extraction cylinders

The extraction cylinder has some advantages in comparison with bark peeling and sifting. Wood-boring species developing inside the wood are trapped in addition, the samples integrate the species reared over a whole season, so they are not restricted to the species being present as adults at a specific moment of sampling, and the extraction cylinders do not cause extensive habitat destruction.

It is unknown to what extent the insect development inside the cylinder is affected by changed light and micro-climatic conditions during the trapping period. However, the major disadvantage of the extraction cylinders and similar methods is that the low trapping efficiency makes it difficult to obtain large enough samples for statistical comparison. Furthermore, these methods share the problem of inadequate standardization of samples.

Trunk-window traps

The trapping efficiency did not differ significantly between trunk-window traps and window traps. Certain species associated with polypores were more abundant in trunk-window traps, while window traps captured more species of Staphylinidae and a higher number of individuals of some species. Most other comparisons of species richness or number of specimens did not show significant differences between these trap models.

Similar to earlier studies (Kaila et al., 1994; Økland & Hågvar, 1994), the present study indicated that the fruiting bodies of polypores function as "attraction centres", and that the majority of the trapped species do not develop in these fruiting bodies. However, the captures of beetles in trunk-window traps are affected by the type of host substrate, such as polypore species, tree species, whether the tree is dead or alive (Kaila et al., 1994); and the developmental stage of the sporocarp (Økland & Hågvar, 1994). For example, trunk-window traps would be expected to show a higher trapping efficiency than window traps when *Fomes fomentarius* (L. ex Fr.) Kickx on dead birches are used instead of *Fomitopsis pinicola* on dead spruces (Kaila et al. 1994).

The trunk-window traps have to be placed where suitable substrates are available in the landscape. Depending on the distribution of the actual substrates (polypores, dead tree trunks), the traps would usually be placed in varying densities per area, and in local sites with varying densities of the actual substrates. Even when exactly the same type of host substrate is used, the sample in each trap may depend on the attraction of other substrates of similar type in the near surroundings (Kaila, 1993). Since the population of attracted specimens are divided between the available sporocarps in a site, the number of similar sporocarps in the near surroundings is assumed to affect the number of specimens attracted to each sporocarp. Furthermore, the species richness in the traps is assumed to be positively correlated with the size of the sampling area, since wide-spread traps may attract beetles from a greater number of habitats.

Different sources of variation influence the trunk-window samples, but their relative contributions are unknown. Thus, trunk-window traps are suitable for faunistic comparisons between various substrates, provided that other environmental variables do not vary systematically, e.g., when all samples belong to the same forest locality (Kaila et al., 1994). Comparisons of different forest environments by means of some standardized samples of trunk-window traps may be more difficult. Firstly, the standardized substrate should be available for mounting traps in comparable numbers in the different forest environments. Secondly, the sampling area and the density of trap substrates should be of comparable sizes, or their contributions to the variation in trap captures should be quantified and corrected for.

Window traps

The baiting effect of wood or polypore substrates may be avoided by the window traps, which may be placed randomly and independent of these substrates. This method is efficient for trapping saproxylic beetles, though the species composition may differ somewhat from that of trunk-window traps. Such differences may be ascribed to the specific patterns of flight and movements for individual species. However, some differences in single species may have resulted by chance, because of the large sample variation and relatively small sample sizes.

Certain species were absent in window traps, but occurred in other trap types (Table 5). They are assumed to avoid the window traps hanging 0.7–1.0 m above ground. Some of the species only found in trunk-window traps or extraction cylinders are poor fliers, and are most often moving on the ground (Table 5). *Malthodes guttifer* Kiesenwetter was numerous in malaise traps, but was absent in all window traps (Table 5). The reason may be that this species flies near the ground or wooden substrates, below the level of the window traps. However, the behaviour of migration and trivial flights (Dingle, 1972) has not been studied for most of the actual species.

Even when traps are operated within the same areas, the grain size (= the area of sampling; Wiens, 1989) may differ considerably between trap models. In the sites lying 900 m apart, extraction cylinders yielded clearly different species-per-trap curves (Fig. 3A), probably because one of the sites contained a larger proportion of deeply decayed wood richer in beetle species. A correspondingly large difference was not found for window traps, which yielded almost equal species-per-trap curves in sites 1 and 2 (Fig. 3C). Both present and former results (Siitonen, 1994; Økland et al., 1996) indicate that substrate conditions near the window traps have little influence on the catches. Apparently, window traps capture flight-active beetles from a relatively wide area of the forest. A slight difference between the sites was found for trunk-window traps, which are affected by both the "air plankton" and the local substrates associated with each trap.

The influence on local window trap captures was gradually improved by increasing the spatial scale of recording decaying wood (Fig. 4), probably due to the high mobility of many beetle species. Apparently, the maximum influence was reached at about 30 ha. However, the area of influence is supposed to vary with landscape structures and beetle assemblages of the various districts. Even an optimal scale of recording decaying wood gave a relatively low influence on the trap captures, probably due to large variation between samples and local sites. Neighbouring sites with similar scores in ecological variables may show marked differences in species richness and abundance of single species (Økland et al., 1996). Such differences may reflect factors which are difficult to quantify, e.g. variations in micro-climate (light, moisture, air currents etc.) and heterogeneous distribution of breeding substrates. While one site usually gives a poor estimate, the saproxylic beetle fauna of a larger area may be better estimated by integrating several traps from different sites.

CONCLUSIONS

A low trapping efficiency of extraction cylinders makes it difficult to aquire sufficient material for statistical testing. A high trapping efficiency was found both for window traps and trunk-window traps. Trapping efficiency and selectivity of trunk-window traps depend on the substrate under the trap. This type of trap is suitable for comparison of different substrates within the same forest environment, while comparative studies of different forest environments are more difficult due to baiting effects. Window trap captures are suitable for comparing different forest environments, but are related to ecological conditions over wide areas, and are almost unaffected by substrate conditions in the near surroundings of the traps. If certain species avoiding the window traps are to be included, other unbaited trap models should be operated in combination with the window traps, e.g. malaise traps (Townes, 1962) and pitfall traps. In all of the present trap types, a large sampling effort is necessary due to large sample variations.

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